

Ants (Hymenoptera: Formicidae) from Burmese Amber

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Abstract—Ants from Burmese amber are described: two new genera with one new species each, *Haidomyrmex cerberus* (Sphecomyrminae) and *Burmomyrma rossi* (inc. subfam.). Systematic position and bionomy of new taxa are discussed, as well as the age of the Burmese amber.

Looking through the collection of Burmese amber in the Natural History Museum, London (BMNH), Prof A.P. Rasnitsyn revealed three insect inclusions provisionally identified as ants. Formicoids were previously unknown from this amber. The age of Burmese amber is disputable, but it is certainly not younger than the Middle Eocene (Cockerell, 1922). Few fossil ants are known from beds older than the Late Eocene, so the Burmese material is of special interest. All three inclusions studied are undoubtedly Formicidae. *Haidomyrmex cerberus* sp. nov. described below is an extremely specialized member of the Subfamily Sphecomyrminae; the other two specimens are too poorly preserved to determine their exact systematic position.

Earlier we placed all known Mesozoic Formicoidea into the extinct families Armaniidae and Sphecomyrminidae of the Superfamily Formicoidea (Dlussky, 1983, 1987; Dlussky and Fedoseeva, 1988). In the recently published macrorevision of ants (Bolton, 1994), all formicoids are treated as a single family, and the following extinct subfamilies are included along with extant subfamilies: Armaniinae Dlussky, 1983, Formicinae Lutz, 1968, and Sphecomyrminae Wilson et Brown, 1967. In that there are no objective criteria of family or subfamily, and because Bolton's book will be the basic manual on ant taxonomy for many years, we accept his classification and will use it hereafter.

Family Formicidae Latreille, 1802

Subfamily Sphecomyrminae Wilson et Brown, 1967

Genus *Haidomyrmex* Dlussky, gen. nov.

Etymology. From Greek *Haidos* (Hades, the abode of the dead) and *myrmica* (ant).

Type species. *H. cerberus* sp. nov.

Diagnosis. Wingless female. Antennae with rather short scape (nearly as long as three basal segments of funiculus together), first and second segments of funiculus short (a little longer than wide), third one longest, following ones gradually shortening towards apex. Frontal lobes absent and antennal bases free. Frons with longitudinal carina. Clypeus bent under, forming an angle with frontal plane of cranium. Genae

unusually extended, forming concave space between anterior margin of clypeus and bases of mandibles (absent in all other Formicoidea known). Mandibles lacking masticatory margin, very large, L-shaped (elbowed at right angle); with a tooth at elbow and acute tip, both directed medially. Eyes well developed. Ocelli reduced to pit-like trace.

Mesonotum with scutum and scutellum separated. Propodeum rounded in profile. Metapleural glands present. Trochanters of all legs obviously one-segmented. Middle and hind tibiae with two spurs, hind ones with one spur simple and another pectinate. Claws with extra tooth. Waist one-segmented. Petiole nodiform, with short but distinct anterior cylindrical part, posteriorly narrowed and clearly separated from gaster, with small anteroventral tooth. Judging from first gastral segment (the only preserved), gaster without constriction and tubular articulation between first and second segments.

Species composition. Monobasic.

Comparison. Differs from all known Formicidae, both recent and fossil, by the very peculiar structure of crano-mandibular system. Although long mandibles without a distinct masticatory margin occur in various recent ants, they never appear L-shaped. Elongation of mandibular muscles in ants with specialized mandibles results from hypertrophy of the posterior head, usually of the occipital angles, whereas in *Haidomyrmex*, the forehead is elongated, thus forming a space between the clypeus and mandibles; this is not encountered in other known Formicidae.

Systematic position. The presence of metapleural glands and clearly separated petiole indicate, beyond doubt, that the new genus belongs to the Family Formicidae. Antennae are of sphecoide type, like in the Armaniinae or Sphecomyrminae, and distinct from geniculate antennae of remaining ants. Scape is relatively shorter than in *Sphecomyrma freyi* Wilson et Brown, but longer than in the Armaniinae. At the same time, the second segment of funiculus is shortened, third longest, and the fourth through seventh (more distal ones not preserved) shorten gradually towards apex.

In the Armaniinae, *S. freyi*, *Cretomyrma* Dlussky, and males of primitive ants the second segment of funiculus is the longest, and the following ones gradually become shorter towards apex, whereas in the females and workers of other ants the segments of funiculus from the second one usually become longer towards the apex, as a rule the apical one being the longest. Antennae untypical for ants are described also in another sphecomyrmine, *Sphecomyrma canadensis* Wilson (Wilson, 1985), having first and fifth segments of funiculus the longest and 6–11th ones gradually shortening towards apex.

Mandibles of *Haidomyrmex*, although very specialized, are also derivable from those of the Armaniinae and Sphecomyrminae (bidentate, of sphecoid type), rather than from leptanilloid mandibles, which are the most primitive for recent ants (Dlussky and Fedoseeva, 1988; at least tridentate, with developed masticatory margin). Wing reduction combined with retention of rudimentary scutellum and the shortened scape (antennae wasp-like) bring the new genus together with other known females of the Sphecomyrminae (*Sphecomyrma* Wilson et Brown, *Cretomyrma*). Paired spurs of hind tibiae (one of them pectinate) and claws with an extra tooth are characteristic of Mesozoic formicoids and primitive groups of recent ants (Myrmecinae, Nothomyrmecinae, Pseudomyrmecinae, Ecitoninae, many Ponerinae). So all these characters compel us to consider *Haidomyrmex* as a specialized member of the Sphecomyrminae. The only objection to this assignment is the loss of ocelli. Ocelli are present in *Sphecomyrma* and primitive recent ants (Nothomyrmecinae, Myrmecinae); however, their reduction, quite common in ants, took place independently in several subfamilies (Pseudomyrmecinae, Dolichoderinae, Formicinae) and can also be expected to have occurred in the Sphecomyrminae.

Remarks. The salient feature of *Haidomyrmex* is the very peculiar structure of the head and mandibles. Its crano-mandibular system is clearly trap-like, analogous to those of many ants (Ponerinae: Odontomachini; Myrmicinae: Dacetini; Formicinae: Myrmotetartini) but designed differently. Long hairs at the sides of the clypeus evidently performed the same function as signalling hairs of some *Myrmoteras* Forel (Agosti, 1992): when the hair touches prey, ant jaws close instantly and grip it. Trap-like crano-mandibular system originates in predatory ants specialized as hunters for large (compared to their own size), moving prey, and the prey spectrum of such predators is usually quite restricted (Wilson, 1953; Brown and Wilson, 1959; Dlussky, 1993). Apical tooth and extra tooth at the elbow of mandible are widely separated (by ca. 0.5 mm), evidence that *Haidomyrmex* preyed on large (compared to its body length, 5 mm) invertebrates with elongate body, probably insect larvae or small myriapods.

Our earlier analysis of functional morphology of the Upper Cretaceous formicoids (Dlussky, 1983) demon-

strated that, on account of mandibular structure, Armaniinae and Sphecomyrminae did not build true nests and could use only ready cavities. Their antennal structure indicates that they could not manipulate small objects, i.e., care for eggs and young larvae, hunt for small prey, etc. Hence, either they could be parasites, or their females hunted for large prey and transported it to larvae living in the nest. However, the former supposition seemed less probable to us, because the development of metapleural glands excreting bactericide substance is most likely correlated with the possession of a nest. Therefore, based upon morphological data, the Upper Cretaceous formicoids presumably hunted for relatively large prey and transported it into natural cavities in the soil or dead wood used as nests. Quite probably, primitive sociality had arisen within these groups, but not true sociality requiring precise manipulations of the brood.

In our opinion, the new find confirms the suggestion regarding semisociality of the Sphecomyrminae. *Haidomyrmex* could not have been a highly social insect for the same reasons as the Upper Cretaceous Formicoidea known earlier. Its antennae, even less geniculate than in the *Sphecomyrma*, were inappropriate for fine manipulations of the brood; its mandibles were even less suitable for nest constructing. At the same time, such a crano-mandibular system could have arisen only in a specialized hunter providing its progeny with food, and not in a female parasite. Judging from the damage characteristic of already dead ants, the holotype of *H. cerberus* was embedded in the resin after its death and desiccation; in the same piece of amber there is a cocoon similar to an ant cocoon, but somewhat larger than the described *H. cerberus* specimen should be. Since ants usually carry the dead individuals and remove cocoons from the nest, the above facts could agree with the presumed semisociality, along with the clear trend towards "formicoidization" of the antennae in the *Haidomyrmex* and *S. canadensis* (expressed in the changed length ratio of segments of funiculus, rather than in the elongated scape).

Nevertheless, conclusive evidence that the Sphecomyrminae were truly social will be resolved only when presumably conspecific alate and wingless females of these insects are found in the same deposits. The opinion that *Armania* Dlussky are females and *Sphecomyrma* are workers of the same genus (Wilson, 1985, 1987) is open to criticism: these insects differ strikingly in the structure of their antennae and petiole and, moreover, are separated by a ten million year interval. Wilson's statement that the gaster in worker ants is always more compactized than in females of solitary Scolioidea (Wilson, 1987) is incorrect: his list of species studied is practically devoid, first, of the workers of Ponerinae, Pseudomyrmecinae, and other ants where the gaster is much less compactized than in *Sphecomyrma*, and second, of scolioid females that actively move over the ground (e.g., Apterygynidae) and have a gaster that is more compact than in *Cretomyrma*.

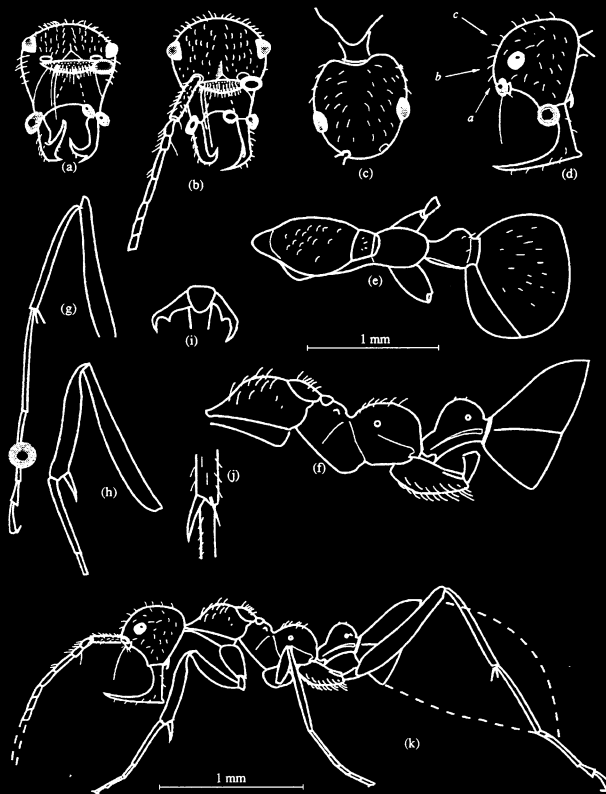


Fig. 1. *Haidomyrmex cerberus* sp. nov., holotype: (a-d) head in different views [view directions for 1a-1c marked with arrows in 1d; (e-f) thorax, petiole, and first gastral segment: (e) in dorsal view; (f) in lateral view; (g) hind leg; (h) fore leg; (i) claws of hind tarsus; (j) spurs on hind tibia; and (k) reconstructed habitus.

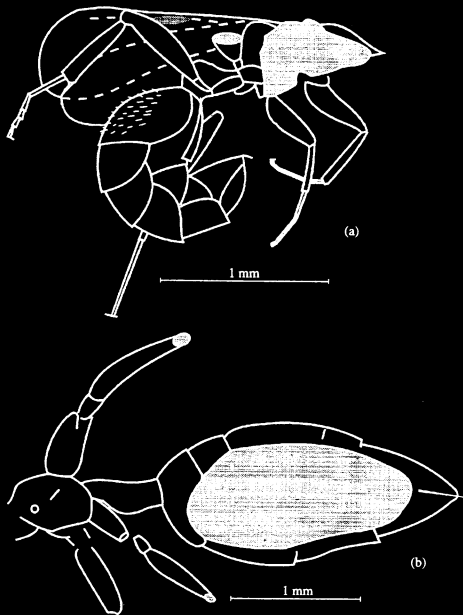


Fig. 2. Ants from Burmese amber: (a) *Burmomyrma rossi* sp. nov., holotype; and (b) undetermined specimen from same amber piece as *Haidomyrmex cerberus* holotype.

Haidomyrmex cerberus Dlussky, sp. nov.

Etymology. From Greek *Cerberus* (mythological watchdog of Hades).

Holotype—BMNH. 20182, head with antennae, thorax, petiole, first segment of gaster, and leg fragments, moderately preserved; Burmese amber; presumably Upper Cretaceous–Lower Eocene.

Description (Fig. 1). Wingless female. Head shape and proportions as in Figs. 1a–1d. Antennal segments ratio: 1(scape) : 2(pedicel) : 3 : 4 : 5 : 6 : 7 = 14 : 4 : 5 : 8 : 7 : 6.5 : 6. More distal segments not preserved. Clypeus with anterior margin feebly convex,

surface densely covered with rather thick setae as long as clypeus itself. Two very long, thin setae at right side of clypeus. Distinct sculpture and decumbent pubescence lacking; all body surface with quite numerous, thin, short, weakly curved, erect hairs. Outer side of scape and of two basal segments of funiculus with numerous suberect hairs.

Measurements, mm. Reconstructed body length about 5; thorax length 1.3; maximal head length 0.7; head width 0.68; scape length 0.35.

Material. Holotype.

Remarks. The reconstruction given is based on drawings of the holotype and of the legs (almost certainly belonging to the same specimen) arranged in natural position. Estimating the size of the missing part of flagellum we assumed that the antennae were 12-segmented. Right side of clypeus bears two very long setae, and the same setae (not preserved) undoubtedly were present at its left side. Contour of gaster is given tentatively, based on the assumption that its shape was similar to that of *Sphecomyrma*, in another ant from the same amber piece, and in the recent *Nothomyrmecia macrops* Clark.

The specimen is fragmented: head, thorax, petiole, and first segment of gaster are well preserved, whereas the legs, one antenna (and distal part of the other), palps, and most of the gaster are broken off. In the same amber piece, the second antenna (also lacking distal segments) and legs (most likely of same specimen) are separately preserved (Figs. 1g-1j). Such damage pattern implies that the insect embedded in resin was already dead, with some parts missing. The same piece of amber contains a hymenopteran cocoon with meconium (about 6 mm long) and strongly oxidized remains of another ant (Fig. 2b). Of the latter specimen, the gaster, legs (partly), and highly deformed petiole and posterior thorax are preserved. The sting, one-segmented waist, and the absence of constriction between first and second gastral segments are clearly visible; hind trochanters are one-segmented. Judging from preserved parts, the specimen was nearly of the same size as the *Haidomyrmex cerberus* holotype, but due to these two having almost no parts in common, it is impossible to confirm or discard that they are conspecific. This insect, undoubtedly of the Family Formicidae, belongs either to the Sphecomyrminae or to primitive ants combining the sting with the one-segmented waist without constriction between the 1st and 2nd gastral segments (Subfamily Nothomyrmecinae or Aneuretinae).

Incertae subfamiliae

Genus *Burmomyrma* Dlussky, gen. nov.

Etymology. From Burma and Greek *myrmica* (ant).

Type species. *B. rossi* sp. nov.

Diagnosis. Alate female. Trochanters of all legs one-segmented. Hind tibia with single spur. Forewings lacking closed cells. Waist one-segmented. Petiole nodiform, with distinct anterior cylindrical part, posteriorly narrowed and clearly separated from gaster. Gaster without constriction and tubular articulation between first and second segments. Sting short, slightly curved upwards.

Species composition. Monobasic.

Comparison. Distinct from all known Formicidae, both recent and fossil, in the absence of closed wing cells combined with one-segmented waist.

Remarks. Systematic position could not be determined reliably due to poor preservation of the only specimen known. Although the sides of the propodeum (and metapleural glands) are not preserved, the sting shape is indicative of the Formicidae (sting is straight or curved downwards in most other Aculeata). The new genus could not be assigned to the Subfamily Armaniinae, characterized by the two-segmented trochanter and no deep constriction between petiole and gaster. Completely reduced venation is recorded in the Leptanillinae and some small Myrmicinae, both having female waist two-segmented and, moreover, Leptanillinae females wingless. The combination of sting, one-segmented waist, and gaster without constriction and tubular articulation between first and second segments in the winged female excludes all the formicid subfamilies except for Sphecomyrminae, Aneuretinae and Nothomyrmecinae. Since the head with antennae and mandibles is not preserved in *Burmomyrma*, its placement in the Sphecomyrminae could not be excluded (although alate sphecomyrmine females are still unknown). In our opinion, the new genus most likely belongs to the Subfamily Aneuretinae.

Burmomyrma rossi Dlussky, sp. nov.

Etymology. After the British paleontologist A.J. Ross.

Holotype—BMNH. 19125, a partly preserved, strongly oxidized specimen (gaster, petiole, legs, wings, and part of thorax preserved); Burmese amber; presumably Upper Cretaceous–Lower Eocene.

Description (Fig. 2a). Alate female. Propodeum angulate in profile, its sides smooth and shiny. First gastral tergum with numerous, short, straight, erect hairs.

Measurements, mm. Reconstructed body length about 3; thorax length about 1; hind femur length 0.6; petiole length 0.33.

Material. Holotype.

CONCLUSION

All three ants found in the Burmese amber belong to the extinct subfamily Sphecomyrminae and perhaps to the primitive extant subfamilies Aneuretinae or Nothomyrmecinae. Up to now the Sphecomyrminae were known only from the Upper Cretaceous (Dlussky, 1987). All Paleocene ants belong to the extant subfamilies Aneuretinae, Dolichoderinae, Formicinae, Ponerinae and Myrmecinae (Dlussky, 1988; Hölldobler and Wilson, 1990; Bolton, 1994); in the Lower Eocene Myrmicinae are also recorded (Wilson, 1985). Aneuretinae and Nothomyrmecinae, considered the most primitive living ants (along with the tribe Amblyoponini of Ponerinae), are represented with one species each in the modern fauna: *Aneuretus semoni* Em. (Sri Lanka) and *Nothomyrmecia macrops* Clark (Australia). The Nothomyrmecinae are absent from the fossil

record, whereas the Aneuretinae are described from the Paleocene (Sakhalin amber; one monobasic genus) and the Late Eocene (Baltic amber; two monobasic genera) (Wheeler, 1915; Dlussky, 1988). The quite archaic composition of Burmese amber ant fauna indicates either the Late Cretaceous age of Burmese amber, or a relic character of the Paleogene amber-producing biota.

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